Climate conditions and resource availability drive return elevational migrations in a single-brooded insect

David Gutiérrez*[a] · Robert J. Wilson[b]

[a] Área de Biodiversidad y Conservación, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Tulipán s/n, Móstoles, Madrid, ES-28933, Spain

Phone: +34 914888160

[b] College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4PS, UK

* Corresponding author: david.gutierrez@urjc.es

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Abstract Seasonal elevational migrations have important implications for life-history evolution, and ecological responses to environmental change. However, evidence is still scarce for their existence and potential causes for most species, particularly invertebrates. We tested the extent to which seasonal abundance patterns in central Spain for overwintering (breeding) and summer (non-breeding) individuals of the butterfly *Gonepteryx rhamni* were consistent with three hypotheses explaining elevational migration: resource limitation (host plant and flower availability), physiological constraints of weather (maximum temperatures) and habitat limitation (forest cover for overwintering). For overwintering adults, abundance was positively associated with host plant density during two intensive survey seasons (2007-2008), and the elevational distribution was relatively stable over a seven-year period (2006-2012). The elevational distribution of summer adults was highly variable, apparently related both to temperature and habitat type. Sites occupied by adults in summer were on average 3°C cooler than their breeding sites, and abundance showed negative associations with summer temperature, and positive associations with forest cover and host plant density in 2007 and 2008. The results suggest that the extent of uphill migration in summer could be driven by different factors depending on the year, mostly consistent with physiological constraint and habitat limitation hypotheses. In contrast, the patterns for overwintering adults suggest that downhill migration can be explained by resource availability. Climate change could generate bottlenecks in the populations of elevational migrant species by constraining the area of specific seasonal habitat networks, or reducing the proximity of environments used at different times of year.

Keywords Climate change · elevational distribution · *Gonepteryx rhamni* · Lepidoptera · seasonal movements

Introduction

Animal migration involves costs and benefits: potential costs include energetic expenses, increased predation risk and reproductive costs, whereas potential benefits include increased survival and reproduction due to exploitation of new resources and avoidance of adverse environmental conditions (Rankin and Burchsted 1992). Migration is expected to evolve only under circumstances in which remaining in natal habitat would be detrimental relative to migrating to a different site (Southwood 1977; Rankin and Burchsted 1992). Migration has been classified in different ways depending on the organism, and spatial or temporal attributes (Dingle and Drake 2007). Typical migrations involve seasonal displacements over hundreds of km between high-latitude summer habitats and low-latitude spring habitats (e.g. Chapman et al. 2012). Depending on the life cycle duration, organisms may breed multiple times within a season producing several generations as populations migrate polewards during spring and summer, and equatorwards during autumn, or alternatively the same individuals may perform the complete round trip (Ramenofsky and Wingfield 2007).

Organisms also show shorter-distance seasonal movements over elevational gradients called elevational migrations. Elevational migrations have been reported from nearly all continents and from several vertebrate and insect taxa, but most evidence is based on birds (McGuire and Boyle 2013). Nevertheless, potential hypotheses explaining bird elevational migration are applicable to other taxa, since they involve resource availability (e.g. Boyle 2010), physiological constraints of weather (e.g. Boyle et al. 2010), predation risk (e.g. Boyle 2008), habitat limitation, and competition for mates (McGuire and Boyle 2013).

Elevational migration has been documented through different methods with different discriminatory power (McGuire and Boyle 2013). Ideally, telemetry of animals will provide spatially and temporally detailed movement information at an individual level (e.g. Norbu et al. 2013). This approach is feasible for some vertebrates, but in the case of many insects, the combination of small sizes, short life cycle, large populations and relatively high flying speed make it difficult to follow individuals (Osborne et al. 2002; but see Urquhart and Urquhart 1978; Wikelski et al. 2006).

Alternatively, elevational migration can be documented through abundance or distribution surveys at multiple elevations and periods (McGuire and Boyle 2013). Then, correlative distribution models can be applied to assess the importance of different variables in determining elevational shifts between periods. This approach has been successfully applied to several species and provided important clues in relation to the drivers of elevational migrations (e.g. Brambilla et al. 2012; Marini et al. 2013).

The importance of seasonal migration to the life-cycles of some Lepidoptera is well established (e.g. Williams 1930). The monarch butterfly *Danaus plexippus* exemplifies the typical insect engaged in mass latitudinal migrations over long distances (e.g. Urquhart and Urquhart 1978), and latitudinal migrations of other Lepidoptera at Temperate latitudes have been well documented (e.g. Mikkola 2003; Stefanescu et al. 2007, 2013; Brattström et al. 2010; Chapman et al. 2012). Elevational migrations have been reported for several Lepidoptera species (e.g. Larsen 1976, 1982; Shapiro 1973, 1974a, b, 1975, 1980, Stefanescu 2001), but in most cases, no explicit assessment of potential hypotheses explaining the phenomenon has been made. One exception is a study on the butterfly *Vanessa atalanta*, in which the resource availability hypothesis was supported (Stefanescu 2001).

In this paper, we test the resource availability, physiological constraints of weather, and habitat limitation hypotheses as potential explanations for uphill and downhill movements of the brimstone butterfly *Gonepteryx rhamni* (L.), in a mountain area in Spain. This species is particularly appropriate to study elevational migrations because it has a relatively high mobility (Gutiérrez and Thomas 2000), and regional movements between hibernating and breeding areas have been hypothesised to occur along elevational gradients (Larsen 1976, 1982; García-Barros et al. 2013). *G. rhamni* is a single-brooded species which develops from egg to adult in spring and has a non-reproductive period in summer until hibernation, after which the mating season occurs the following spring (Wiklund et al. 1996). In our study, we first determine the extent of the migration by examining abundance patterns over elevation for overwintering (breeding) and summer (non-breeding) individuals. Then, we model separately the abundance of overwintering and summer individuals based on environmental resources and conditions to assess the relevance of the three proposed hypotheses. We expected stronger support for the resource availability hypothesis (based on host plant abundance) for overwintering individuals,

because of the requirement for breeding sites. In contrast, the distribution of summer (non-breeding) individuals could have been driven by physiological constraints (temperature), habitat limitation (e.g. overwintering sites) and/or resource availability (e.g. flower abundance).

Materials and methods

Study system

Gonepteryx rhamni (L.) is a widespread species in Europe, whose larvae feed on shrubs from the family Rhamnaceae. It has one adult generation per year (emerging in June-August), and hibernates as an adult (resuming activity in late winter) (Tolman and Lewington 1997). In Spain, *G. rhamni* is a relatively common species, but in the southern half of the country the populations are more frequent in mountains (García-Barros et al. 2004). There are no detailed records of overwintering habitats for *G. rhamni* in the study area, but wooded areas have been suggested elsewhere in Europe (Pollard and Hall 1980).

The Sierra de Guadarrama (central Spain) is an approximately 100 x 30 km mountain range located at 40°45' N 4°00' W. The mountain range is bordered by plains with elevations of c. 700 m (to the north) and c. 500 m (to the south) and reaches a maximum elevation of 2428 m (Fig. 1). The main regional host plants reported for *G. rhamni* are *Frangula alnus* Mill. and *Rhamnus cathartica* L. (based on oviposition and larval records, D. Gutiérrez and R.J. Wilson, unpublished data), although at least two other species from the family Rhamnaceae occur in the study area (*R. lycioides* L. and *R. alaternus* L.).

Elevational abundance of *G. rhamni*

To study the elevational patterns of *G. rhamni* abundance, butterflies (including *G. rhamni*, if present) were counted in 2007 and 2008 on standardised 500 m long by 5 m wide transects at 40 sites ranging 558-2251 m in elevation. A subsample of 24 of those 40 sites were also visited following identical methodology in 2006 and 2009-2012 to examine the temporal variability of elevational patterns. Transects were walked during suitable conditions for butterfly activity (sunshine and no more than

light wind, between 10:00 h and 17:00 h European Summer Time; Pollard and Yates, 1993), every two weeks from April to October in 2006, and from March to October since 2007. Due to snow cover and unsuitable weather, transect walking started later than March or April in some years at sites above 1700-1800 m.

During counts, we explicitly distinguished overwintering from summer *G. rhamni* adults based on wing condition. In the Sierra de Guadarrama, overwintering adults fly from early March (some occasional records in February in warm winters) to June, whereas summer adults fly from June to October. Because overwintering adults are increasingly worn over the season, they are easily distinguished from recently emerged summer adults (in excellent condition) over the potential overlap in flight period of both generations in June. Sexes were recorded separately in the field but were pooled together for analyses, because of no obvious sex-related patterns and a much smaller sample size for females. For each site and year, overwintering and summer adult abundances were calculated as the sum of all counts of overwintering and summer individuals over the season. During transect walking and additional visits to sites, information on reproductive (oviposition) and feeding (nectaring) behaviour was also recorded.

Environmental variables

Universal Transverse Mercator (UTM) coordinates were recorded c. every 100 m along transects using a handheld Garmin GPS unit, and were used to plot transects in a geographic information system (ArcGIS) (ESRI 2001). The average elevation of 100 m cells intercepted by transects was determined using a digital elevation model (Farr et al. 2007).

To examine potential determinants of the elevational distribution of overwintering and summer adults, we collected environmental variables from the field (spring and summer temperatures, host plant density, summer flower abundance) and from digital layers (forest cover). The biological significance of each variable is detailed in Table 1.

For the period 2006-2012, hourly air temperature was recorded by HOBO H8 Pro HR/Temp and U23 HR/Temp loggers in semi-shaded conditions at each of the 40 sampling sites (one logger per

153 site). Twenty data loggers were started in spring 2004 (20 of the 40 sampling sites) and twenty in
154 spring 2006. Mechanical failure or damage to some data loggers due to snow, animals or human
155 interference, generated gaps of variable duration in the data set. Therefore daily average, maximum
156 and minimum temperature time series had to be interpolated for some loggers to subsequently estimate
157 spring and summer temperatures (Electronic supplementary material, ESM, Appendix S1).
158 Interpolated daily maximum temperature data were used to calculate both monthly mean maximum
159 temperatures and subsequently spring (March-May) and summer (June-August) mean maximum
160 temperatures. Seasonal temperatures were based on maximum instead of mean daily temperatures
161 because they more likely represent the conditions experienced by a daylight flying insect like *G.*
162 *rhamni* (e.g. Wiklund et al. 1996). Spring and summer mean maximum temperatures were highly
163 correlated, respectively, with spring and summer mean temperatures both in 2007 and 2008 (all four
164 Spearman's rank correlation coefficients r_s ranged 0.92-0.97).
165 The abundance of host plants was estimated at each of the 40 transect sites in 2006, with some
166 additional records in 2008. The route of the 500 m transect was followed in August–September 2006
167 and the number of plants of *F. alnus*, *R. cathartica* and *R. lycioides* (*R. alaternus* was absent from
168 sampling sites) that occurred in the 5 m wide butterfly transect was recorded, to give a density of each
169 species per 0.25 ha (500 × 5 m). If none of the plant species were present in the 5 m wide transect,
170 then the transect was repeated with increasing widths of 10 m, 20 m, and up to a maximum of 50 m
171 width (i.e. 25 m on either side of the recorder). In this case, host plant density per 0.25 ha was
172 estimated based on the increased transect width. Host plant species were considered present at a site if
173 they were found in transects of ≤ 50 m wide (Merrill et al. 2008). To test for temporal variability in
174 host plant density, the number of plants that occurred in the 5 m wide transect was counted again in
175 2009.
176 Summer flower abundance was estimated during the summer adult flight peak in 2007 and 2008 by
177 taking twenty 0.25 m^2 quadrats (50 x 50 cm) at 25 m intervals along each transect. We set quadrats in
178 late July 2007 and late July-early August in 2008, and flower abundance was estimated by counting
179 the number of 2.5 x 2.5 cm sub-quadrats (100 per quadrat) containing more than 4 cm^2 surface of

flowers. Data from elsewhere in Spain show that *G. rhamni* is not a specialist flower visitor (Stefanescu and Traveset 2009), and therefore we considered that all flowering species could be potential nectar sources.

Forest cover was estimated from regional land-cover maps obtained in vector format at 1:50,000 scale (Ministerio de Medio Ambiente, 2000, 2002a, b, 2003), which showed good agreement for all transects with our own field observations of general vegetation type (Gutiérrez Illán et al. 2010). Vector data from the land-cover maps (minimum cartographic unit 2.25 ha) were used to determine the proportional contribution of total forest cover to each 100-m grid cell. Forest cover for each site was estimated as the mean for 100 m grid cells intercepted by each transect.

Elevational abundance models

To analyse *G. rhamni* abundance, we applied Generalised Linear Models (GLMs) with a quasi-likelihood estimation of regression coefficients using a log-link and setting the variance equal to mean (quasi-Poisson regression, McCullagh and Nelder 1989). The information-theoretic approach (Burnham and Anderson 2002) was used to model *G. rhamni* abundance. First, elevational trends in abundance for overwintering and summer individuals in 2007 and 2008 were analysed, and second, more complex models including environmental variables were tested to explain the observed trends in abundance over the elevational gradient. For analysing elevational trends in abundance, linear and quadratic models including elevation only were fitted. The more complex models for potential explanatory factors included three candidate variables (spring mean maximum temperatures, host plant density, forest cover) for overwintering individuals and four variables (summer mean maximum temperatures, host plant density, flower abundance, forest cover) for summer individuals (Table 1). Pair-wise correlations between the independent variables had absolute values lower than 0.7 (commonly applied threshold for testing for collinearity, Dormann et al. 2013). Linear and quadratic terms for the environmental condition variables and only linear terms for the strictly resource variables were included (Table 1). Confidence sets were based on the Akaike Information Criterion for small sample size ($QAIC_c$; Burnham and Anderson 2002; ESM, Appendix S2).

Following model selection, model-averaging was used to obtain model coefficients based on the confidence sets (Burnham and Anderson 2002). This approach incorporates model selection uncertainty whilst weighting the influence of each model by the strength of its supporting evidence. Model-averaged coefficients were calculated by weighting using Akaike weights, and averaging coefficients over all models in the confidence sets. Averaging over all models means that in those cases in which a given variable was not included in a particular model, its coefficient value was set to zero. Relative variable importance (parameter lying in the range 0-1, which provides evidence about the relevance of each variable relative to the others) was calculated as the sum of Akaike weights across all models in the confidence set that contain that variable. Model selection and averaging were performed using 'MuMIn' package (R Development Core Team 2012; Bartoń 2012).

Spatial autocorrelation can influence the reliability of ecological analyses, and potentially generates models containing a relatively larger number of predictors in information theoretic approaches (e.g. Diniz-Filho et al. 2008). To test for spatial autocorrelation, all-directional correlograms (Legendre and Legendre 1998) were generated for abundance data of overwintering and summer adults in 2007 and 2008 by plotting values of Geary's *c* coefficient (recommended for variables departing from normality) against Euclidean distances between sites. Geary's *c* calculation and testing for significance were performed using 4999 Monte Carlo permutations in Excel add-in Rookcase (Sawada 1999). No correlogram was globally significant, suggesting that spatial autocorrelation in *G. rhamni* abundance data was negligible.

After identifying the model confidence sets for *G. rhamni* abundance, hierarchical partitioning (HP) was used to assess independent and joint effects of each parameter in single models with all parameters (Chevan and Sutherland 1991; Mac Nally 1996). Poisson regression and log-likelihood as the goodness-of-fit measure were used for HP calculations, and statistical significance of the independent contributions was tested by a randomization routine (1000 permutations) based on Z-scores (Mac Nally 2002). HP was conducted using the 'hier.part' package (Mac Nally and Walsh 2004). One of the limitations of HP as currently implemented in the 'hier.part package' is that it depends on monotonic relationships between the response and predictor variables. However, all

relationships of abundances of overwintering and summer adults against environmental variables were monotonic (see below) and hence this was not a major problem.

Temporal variability in elevational patterns

To examine variability in elevational abundance patterns over time, we used *G. rhamni* abundance data collected at 24 sites over a 7-year period (2006-2012). Mean elevation was calculated separately for overwintering and summer individuals each year by averaging the elevations of all sites where *G. rhamni* was present, weighted by abundance at each site. To test the potential dependency over time of elevational abundance patterns on climate conditions, mean elevations of overwintering and summer adults were compared with spring and summer mean maximum temperatures, respectively, using Spearman's rank correlation coefficients (r_s). To examine the importance of temperature, host plant density and forest cover on *G. rhamni* abundance in different years, quasi-Poisson regressions were performed based on the 24-site data set and using the same approach as for the 40-site data set.

To examine the extent to which *G. rhamni* adults maintain the temperatures experienced from spring to summer, weighted mean temperature was calculated separately for overwintering (March-May temperatures) and summer (June-August temperatures) individuals using the same approach as for weighted mean elevation. Finally, to determine the extent to which the breeding sites have greater temperatures in summer than those experienced by adult butterflies, mean temperatures were calculated at sites where larval host plants were present.

Results

A total of 212 overwintering and 116 summer *G. rhamni* individuals were counted in 2007, and 238 overwintering and 96 summer individuals in 2008. The phenology of overwintering adults was similar in 2007 and 2008, whereas that of summer adults was delayed in 2008 relative to 2007 (Fig. 2). Eight females were recorded ovipositing on *F. alnus* and *R. cathartica* at transect sites; the earliest oviposition record was on 1 April 2011 and the latest on 12 June 2008. A total of 70 nectaring records were collected over 2007-2012 from 16 plant genera from 13 different families, supporting the idea that *G. rhamni* adults are not specialist flower visitors (Stefanescu and Traveset 2009). Mean

maximum and minimum temperatures peaked in July or August depending on site (ESM, Fig. S1). The warmest mean maximum temperature was in July at the lowest site (c. 38°C) and in August at the highest site (c. 20°C).

Elevational patterns

In 2007, overwintering adults were recorded at 23 sites (739-1635 m elevation range) and summer adults at 25 sites (1020-2251 m); in 2008, overwintering adults were recorded at 23 sites (844-1925 m) and summer adults at 21 sites (1056-1976 m). Maximum local abundances were 39 overwintering (at 1270 m) and 22 summer (at 1499 m) individuals in 2007, and 54 overwintering (at 960 m) and 14 summer (at 1270 and 1327 m) individuals in 2008 (Fig. 3).

There were quadratic relationships between abundance and elevation for overwintering and summer individuals in both study years (Table 2, Fig. 3). Models including only the linear term for elevation had a $QAIC_c$ difference of more than 6 from the quadratic (best) model (indicating that they were not well supported; Burnham and Anderson 2002; Richards 2008), in all four cases. Modelled maximum abundance for overwintering individuals peaked at 1214 m in 2007 and 1152 m in 2008, and for summer individuals at 1604 m in 2007 and 1387 m in 2008. Abundances of overwintering and summer adults were not significantly correlated in 2007 ($r_s = 0.23$, $P = 0.158$, $N = 40$), but they were in 2008 ($r_s = 0.46$, $P = 0.003$, $N = 40$). No significant correlation was found between summer adult abundance in 2007 and overwintering adult abundance in 2008 (the same generation at different times) ($r_s = 0.14$, $P = 0.377$, $N = 40$).

A total of 16 transect sites included potential larval host plants in 2006, with the three host plants (*F. alnus*, *R. cathartica* and *R. lycioides*) present, respectively, at nine, nine and one of the transect sites. The distribution of *R. lycioides* was restricted to the lowest site (558 m) of the study area (additional field searches showed that *R. cathartica* also occurs below 600 m), but all host plants were absent from the highest elevations (maximum elevation: 1504 m for *F. alnus*). Additional field searches at 90 sites included in a related study (Gutiérrez Illán et al. 2010) did not encounter any of the host plants above 1504 m. Hence, there was a c. 750 m elevational gap (1504-2251 m) without host

plants in the study area (Fig. 3). Mean elevation was 1208 m for all sites containing host plants. There was a highly significant positive correlation between host plant density (based on 5 m wide transect data) in 2006 and 2009 (r_s = 0.96, P < 0.001, N = 40), suggesting that this variable was relatively constant in time.

Spring and summer mean maximum temperatures were highly negatively correlated with elevation in both study years. Summer flower abundance had no apparent elevational pattern in any year, and forest cover declined significantly with increased elevation (ESM, Fig. S2).

Weighted mean elevation within each season (at four-week intervals) was relatively stable for overwintering adults in 2007 and 2008 (Fig. 4; see ESM, Fig. S3 for results for males and females separately). However, for summer adults, weighted mean elevation increased over the season in 2007, and increased till August to subsequently decrease in September in 2008.

Abundance models

For the abundance of overwintering adults, model confidence sets consisted of two models both in 2007 and 2008 (Table 3). The final averaged models included positive relationships with host plant density and forest cover (in 2007), and with host plant density and spring mean maximum temperature (in 2008). Relative variable importance was 1 for host plant density in both years, indicating it was the most important variable explaining overwintering adult abundance. Spring mean maximum temperature was also well supported in 2008 (variable importance ≥ 0.9).

For summer adults, the confidence sets consisted of three models both in 2007 and 2008. In 2007, the final model included positive relationships with host plant density and forest cover, and a negative relationship with summer mean maximum temperature. In 2008, the final model included those three variables plus a negative relationship with flower abundance. The most important variables explaining summer adult abundance were summer mean maximum temperature (variable importance 0.86-1) and forest cover (variable importance 0.81-1). Nevertheless, host plant density and flower abundance showed relatively high variable importance values in 2008 (> 0.8).

In hierarchical partitioning, the independent effect of host plant density was the only statistically significant variable for overwintering adults in 2007 and 2008 (Fig. 5). The independent contributions were not significant for the two remaining variables in 2007 or for forest cover in 2008. For summer adults, summer mean maximum temperature had the only statistically significant independent contribution in 2007, but there were significant effects of host plant density and forest cover in 2008. The negative joint contributions of summer mean maximum temperature, forest cover and flower abundance for summer adults (Fig. 5b, d) indicate that the joint action of other variables suppresses or masks the independent contribution of those particular predictors (Chevan and Sutherland 1991; Mac Nally 1996).

Temporal variability in elevational patterns

Weighted mean elevation was consistently higher and more variable for summer than for overwintering adults over the 7-year period (Fig. 6). Summer mean maximum temperatures were on average c. 12°C higher than spring mean maximum temperatures over the elevation gradient (Fig. 6). Spring and summer mean maximum temperatures tended to follow a similar pattern over the 7-year period, but the correlation was not significant (r_s = 0.68, P = 0.094, N = 7). No correlation of overwintering or summer mean elevation of butterfly adults against the corresponding seasonal temperatures was significant (P > 0.5). However, summer mean elevation was significantly positively correlated with summer mean maximum temperature if 2007 (the coldest summer) was excluded from analysis (r_s = 0.83, P = 0.042, N = 6), suggesting that *G. rhamni* adults generally occurred at higher elevations in warmer summers (Fig. 6).

Models based on the 24 sites revealed that host plant density was the most important variable explaining overwintering adult abundance in all years, but spring mean maximum temperature was also included in all models with a positive effect (six years) or quadratic effect (one year) (ESM, Table S1). Summer mean maximum temperature was the most important variable associated with summer adult abundance with negative (three years) or quadratic (two years) effects. Host plant density was

335 positively associated with summer abundance in four years, three of which were relatively cold (ESM,
336 Table S1, Fig. 6).
337 Weighted mean temperatures experienced by overwintering adults in spring ranged 15.4-18.9°C,
338 and by summer adults 23.7-27.4°C. Mean temperatures at host plant sites in spring ranged 15.4-
339 18.4°C, and in summer 26.5-30.4°C. Mean difference between weighted mean temperatures for
340 butterflies and mean temperatures for host plants were +0.5°C in spring and -3°C in summer.
341 Correlations (r_s) between overwintering and summer adult abundances within the same year ranged
342 -0.01-0.58 (N = 24 in all cases), with the only significant coefficient in 2008 (P = 0.003; consistent
343 with the analysis with a larger sample size above). Correlations between summer adult abundance in
344 one year and overwintering adult abundance in the immediately following year ranged 0.04-0.48 (N =
345 24), and they were significant for summer adults 2008-overwintering adults 2009 (P = 0.026) and
346 summer adults 2011-overwintering adults 2012 (P = 0.017), corresponding to years with relatively
347 cold summers (Fig. 6).

348 ## Discussion

349 Our results show marked differences between the elevational abundance patterns for overwintering
350 and summer *G. rhamni* adults. In both intensive study years (2007 and 2008), summer adults were on
351 average at higher sites than overwintering adults, and this pattern was maintained over five additional
352 years in which a smaller number of sites were sampled.

353 ### Migration as a mechanism to explain elevational abundance patterns

354 The differences in abundance patterns for overwintering and summer adults were consistent with
355 seasonal elevational migration by *G. rhamni*. Our oviposition records, albeit relatively limited, were
356 consistent with the univoltine life cycle reported for *G. rhamni* with spring breeding (García-Barros et
357 al. 2013). As a result, the same individuals emerging in summer that migrate uphill must migrate back
358 down to breed the next spring. The steadily higher weighted mean elevation of summer adults until
359 late August suggested that uphill migration was a gradual phenomenon over summer (Fig. 4). The
360 decreased weighted mean elevation of summer adults in September 2008 was consistent with downhill

361 migration in autumn, but this was not supported by 2007 data. Occasional observations of adult *G.*
362 *rhamni* flying down in October and late winter suggest that downhill migration could occur in both
363 periods, but this point would require further research.
364 One intriguing result (found also in the UK, Pollard and Yates 1993) is the fact that the abundance
365 of overwintering individuals based on all sites was larger than that recorded in the previous summer
366 (Table 2 and ESM, Table S1). This is clearly ecologically impossible (assuming that there is no
367 significant immigration from outside the study area at some point in the season) because the number of
368 individuals must decrease during hibernation. The exact reason for this is unknown, but it could be
369 related to differences in behaviour in spring and summer, leading to differences in detectability
370 (Pollard and Yates 1993). Reduced summer activity could also make difficult to quantify potential
371 downhill movement in late summer.
372 Abundance models and hierarchical partitioning suggested that explanations for migration in one
373 direction may not explain return movements in the opposite direction. We tested for effects of resource
374 availability, physiological constraints of weather and habitat limitation (McGuire and Boyle 2013) and
375 found that they were differentially supported for uphill and downhill migrations.
376 Several hypotheses could explain uphill migration of *G. rhamni*. In 2007, the strongest effect
377 explaining summer adult abundance was summer mean maximum temperature (Table 3, Fig. 5), with
378 *G. rhamni* more abundant at cooler sites during the summer period. This is in line with the
379 physiological constraints of weather hypothesis, wherein climatic factors may pose direct challenges
380 to survival (McGuire and Boyle 2013). Central Spain is characterised by a continental Mediterranean
381 climate with extremely hot temperatures in summer exceeding 35°C at lower sites, but much cooler (c.
382 20°C) higher up in the mountains (ESM, Figs S1 and S2). Extremely hot temperatures could affect
383 survival and flight willingness in *G. rhamni*, but demonstrating this would require experimentation
384 (e.g. Pruess 1967). In an experiment with caged individuals, Swedish *G. rhamni* showed higher flight
385 willingness at 23-29°C than at 14-20°C, but temperatures above 29°C were not tested (Wiklund et al.
386 1996). In 2008, the main variables explaining summer adult abundance were host plant density and
387 forest cover. This year showed the smallest difference in elevation between overwintering and summer

388 adults, suggesting reduced elevational migration. The effect of forest cover was consistent with the
389 habitat limitation hypothesis, which in the case of *G. rhamni* could be associated with availability of
390 overwintering sites (Pollard and Hall 1980). Weighted mean elevations for summer adults were much
391 more variable than those for overwintering adults (Fig. 6). This result, along with the different
392 contributions of explanatory variables to abundance models based on 40 and 24-site data sets, suggests
393 that uphill migrations could be driven by different factors depending on the particular year.
394 Specifically, the physiological constraints of weather hypothesis would be expected to be more
395 important in hotter summers. This fact was supported by the positive trend between weighted mean
396 elevation for summer adults and summer mean maximum temperature (Fig. 6) (but we do not have
397 any plausible explanation for the year 2007 outlier), and the negative or quadratic effects (based on 24
398 sites) of summer mean maximum temperature in the warmest years (ESM, Table S1). Surprisingly, the
399 resource availability hypothesis for adults was not supported at all, because summer flower abundance
400 was only included in some models but with a negative effect (Table 3).
401 The hypotheses explaining uphill migration by *G. rhamni* strongly contrast with those supported
402 for other butterfly species. For instance, uphill migration by *V. atalanta* has been suggested as a
403 strategy to track larval resources through space and time (resource availability hypothesis) (Stefanescu
404 2001). Although based on less detailed information, the same hypothesis has also been invoked to
405 explain uphill migration by other species (e.g. Shapiro 1974a, 1975, 1980).
406 Resource availability for early stages apparently drives return downhill migration (either in
407 autumn, or following hibernation) by *G. rhamni* individuals before spring breeding. Host plant density
408 was the most important variable explaining overwintering adult abundance in 2007 and 2008 and in
409 2006-2012 based on the reduced 24-site data set (Table 3, Fig. 5, ESM, Table S1). In addition,
410 weighted mean elevation for overwintering adults was relatively constant over the 7-year study period
411 and close to the mean elevation for host plants, regardless of climatic conditions (Fig. 6). Given the
412 relative host plant specialism of *G. rhamni*, looking for larval host plants is probably one of the
413 strongest evolutionary pressures favouring downhill migration in this species. Failure to do so will
414 result in the highest fitness cost of no breeding at all.

One further hypothesis to explain elevational migration not considered in our study is predation risk, which states that migration has evolved in response to elevational differences in predation pressure (e.g. Boyle 2008). In the case of butterflies, this hypothesis has been discussed in terms of larval parasitism (e.g. Stefanescu et al. 2012). However, this is not applicable to *G. rhamni* because adults do not reproduce in summer. Evaluation of the predation risk hypothesis would require the difficult task of collecting information about adult predators.

Hilltopping (a mating strategy of some insect species in which males occupy prominent topographic features due to female scarcity) has been suggested as a component of uphill migration by some Hymenoptera (Hunt et al. 1999). However, *G. rhamni* is a spring-breeding species with patrolling behaviour, so hilltopping cannot explain the observed distribution of migrant adults in summer.

A final possibility is that differential survival might contribute to the elevational shifts shown in this study. Greater adult abundance at higher sites in summer relative to spring could arise from increasing survival of *G. rhamni* juvenile stages or adults with increasing elevation. However, three findings do not support this possibility as the main explanation: (1) substantial numbers of adults were recorded at elevations above the elevation range of larval host plants; (2) large numbers of individuals were recorded at lower elevations in spring following hibernation; (3) no significant correlation was found between overwintering and summer abundance within the same year for all years but one (2008); if *in situ* survival made a substantial contribution to the abundance of summer adults, some degree of correlation between overwintering and summer abundance would be expected (e.g. Pollard and Greatorex-Davies 1998).

One particularity of *G. rhamni* is that individuals make a return migration to the area from which they bred. This is the most common type of migration in birds and mammals, but has rarely been documented in insects (Holland et al. 2006; but see Samraoui et al. 1998). The best-known case of return latitudinal migration (associated with overwintering areas) is that performed by the best-studied migratory insect, the monarch butterfly (*Danaus plexippus*), but successive broods are involved while progressing northwards (Flockhart et al. 2013). Possible return elevational migrations have been

reported for some butterfly species in other areas with hot and dry summers, including *G. rhamni* (Larsen 1982). In this case, individuals were thought to breed at high elevations in summer and then to migrate downhill in autumn to overwinter (Larsen 1976). This opens questions regarding the extent to which variability in regional climates, resource distributions and seasonality may drive divergent elevational migration patterns within the same species, and the extent to which they may be subject to change in a changing climate. Our results suggest phenotypic plasticity in the extent and timing of return elevational migration by *G. rhamni*, probably linked to the fact that it is a univoltine species with long-lived adults. In this sense, the study of possible migration patterns in other species with similar life cycles could shed light on the life-history and evolution of elevational migration in insects.

The results presented here have some implications in the context of climate change. It was found that *G. rhamni* summer adults occurred at sites which were on average 3°C cooler than breeding (host plant) sites; that summer abundance was sometimes negatively associated with summer mean maximum temperatures; and that higher sites may have been occupied in warmer summers. Furthermore, numbers of post-overwintering adults per site were only significantly correlated with numbers of pre-hibernating adults after two relatively cool summers (2008 and 2011). Assuming that temperature is an important determinant of summer elevational distribution, this evidence suggests that a warming climate could eventually generate a bottleneck in *G. rhamni* populations in the Sierra de Guadarrama through the constraint of its summer habitat network. This is in line with the idea that climate change could affect elevational migrants (Inouye et al. 2000), but through a completely different mechanism to phenological synchrony with resources.

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612

613 **Table 1** List of environmental variables included in the present study, classified by their biological
614 significance. Spring and summer mean maximum temperatures, and summer flower abundance were
615 recorded separately in 2007 and 2008. Host plant density was square-root transformed for analyses to
616 avoid influential effects of individual sites (Zuur et al. 2007)

Environmental variable (units)		Code	Mean (min-max)
Conditions: adult thermoregulation and larval development			
Spring mean maximum temperature (°C)	2007	Sprtmax	13.26 (5.67-20.54)
	2008		13.24 (5.49-21.44)
Summer mean maximum temperature(°C)	2007	Sumtmax	24.52 (16.74-34.45)
	2008		24.91 (17.54-35.90)
Resources: larval host plants and adult nectar sources			
Host plant density (number of plants 0.25 ha^{-1})		Hostpl	2.43 (0-29)
Summer flower abundance (percent cover)	2007	Flowab	3.08 (0-11.25)
	2008		1.64 (0-5.50)
Conditions and resources: conditions and sites for adult overwintering			
Forest cover (proportion cover)		Forest	0.63 (0-1)

617

618 **Table 2** GLMs (quasi-Poisson error and log-link) for the abundance of overwintering and summer *G.*
619 *rhamni* adults in 2007 and 2008 with elevation (km). The total number of individuals (Ind) and
620 coefficients (SE) for elevation and elevation^2 are shown. In the four cases, the quadratic models
621 showed $QAIC_c$ values which were lower by more than 6 units from those for the linear models (not
622 shown). $N = 40$ sites in all cases

Model	Ind	Elevation	Elevation^2	Intercept
Overwintering adults 2007	212	33.52 (8.89)	-13.81 (3.67)	-17.63 (5.32)
Summer adults 2007	116	13.54 (5.28)	-4.22 (1.73)	-9.14 (3.95)
Overwintering adults 2008	238	21.10 (9.57)	-9.16 (4.05)	-9.50 (5.54)
Summer adults 2008	96	26.35 (7.26)	-9.50 (2.62)	-16.52 (5.00)

623

624

Table 3 Confidence set GLMs (quasi-Poisson error and log-link) for the abundance of overwintering and summer *G. rhamni* adults in (a) 2007 and (b) 2008 (*N* = 40 sites in all cases). The table indicates the variables included in the model and the direction of their coefficients (+/-; codes in Table 1); number of parameters (K, including one extra parameter for over-dispersion factor in $QAIC_c$); Akaike Information Criterion for small sample size corrected for over-dispersed count-data ($QAIC_c$); difference in $QAIC_c$ between current and best model ($\Delta QAIC_c$). Relative importance (Imp), model-averaged coefficients (Coef) and unconditional standard errors (SE) for each variable are also shown. Dispersion parameter is for the full model

a) Overwintering adults 2007

Rank	Hostpl	Forest	Intercept	K	$QAIC_c$	$\Delta QAIC_c$	$QAIC_cw$
1	+	+	+	4	56.84	0.00	0.71
2	+		+	3	58.63	1.78	0.29
Imp	1	0.71					
Coef	0.49	0.88	0.27				
SE	0.09	0.66	0.63				

Dispersion parameter = 6.05

Summer adults 2007

Rank	Sumtmax	Hostpl	Forest	Intercept	K	$QAIC_c$	$\Delta QAIC_c$	$QAIC_cw$
1	-		+	+	4	58.44	0.00	0.81
2	-	+		+	4	62.53	4.09	0.10
3	-			+	3	62.80	4.36	0.09
Imp	1	0.10	0.81					
Coef	-0.18	0.02	1.24	4.35				
SE	0.08	0.15	0.67	1.55				

Dispersion parameter = 4.49

638 b) Overwintering adults 2008

Rank	Sprtmax	Hostpl	Intercept	K	$QAIC_c$	$\Delta QAIC_c$	$QAIC_cw$
1	+	+	-	4	59.72	0.00	0.94
2		+	+	3	65.09	5.37	0.06
Imp	0.94	1					
Coef	0.15	0.62	-1.41				
SE	0.06	0.08	1.12				

639 Dispersion parameter = 5.61

640 Summer adults 2008

Rank	Sumtmax	Hostpl	Flowab	Forest	Intercept	K	$QAIC_c$	$\Delta QAIC_c$	$QAIC_cw$
1	-	+	-	+	+	6	79.28	0.00	0.74
2		+	-	+	-	5	82.61	3.33	0.14
3	-	+		+	+	5	83.02	3.74	0.11
Imp	0.86	1	0.89	1					
Coef	-0.09	0.46	-0.28	1.94	1.36				
SE	0.05	0.10	0.14	0.65	1.40				

641 Dispersion parameter = 2.19

642

643 **Figure legends**

644 **Fig. 1** Site distribution for *G. rhamni* in 2006-2012. Squares show 2006-2012 sites (*N* = 24) and
645 circles additional 2007-2008 sites (*N* = 16) for modelling abundance. Filled symbols are sites where *G.*
646 *rhamni* was observed in 2007-2008, open symbols where absent. Elevation bands are shown as 0.25
647 km increments from < 0.75 km (pale grey) to > 2 km (black). The inset map shows the geographical
648 context of the study area in Spain. Georeferencing units are in UTM (30T; ED50)
649
650 **Fig. 2** Phenology of *G. rhamni* overwintering (dashed lines) and summer (solid lines) adults
651 throughout the seasons 2007 (thick lines) and 2008 (thin lines). Phenology data are shown as the sum
652 of all individuals counted at all transects during a given transect fortnight. Dates were calculated as the
653 mean date for all transect counts in a given fortnight
654
655 **Fig. 3** Abundance of *G. rhamni* and density of its host plants with elevation. (a) *G. rhamni* in 2007 and
656 (b) *G. rhamni* in 2008 for overwintering (empty circles, dashed line) and summer (black circles, solid
657 line) adults; (c) host plants (sum of plants of *F. alnus*, *R. cathartica* and *R. lycioides*). Lines plotted
658 based on equations in Table 2. The vertical dashed thin line indicates the maximum elevation at which
659 host plants were recorded
660
661 **Fig. 4** Weighted mean elevation of *G. rhamni* overwintering (dashed lines) and summer (solid lines)
662 adults within season in 2007 (thick lines) and 2008 (thin lines). The horizontal thin lines indicate the
663 mean (solid) and maximum (dashed) elevation at which host plants were recorded. Figures next to
664 symbols are sample sizes.
665
666 **Fig. 5** The independent (black) and joint contribution (white) (given as the percentage of the total
667 variance explained by the model) of the environmental variables estimated from hierarchical
668 partitioning for *G. rhamni* abundance of (a) overwintering adults in 2007, (b) summer adults in 2007,

669 (c) overwintering adults in 2008, and (d) summer adults in 2008. * indicates significant ($P < 0.05$)
670 independent contributions from randomisation tests. Variable codes as in Table 1. $N = 40$ sites in all
671 cases. Note the different y-axis scales
672
673 **Fig. 6** Relationship between *G. rhamni* mean elevation and mean temperature over the period 2006-
674 2012 for (a) overwintering (empty circles) and (b) summer (black circles) adults. Figures next to
675 symbols are years. Horizontal thin lines as in Fig. 4

Figure 1

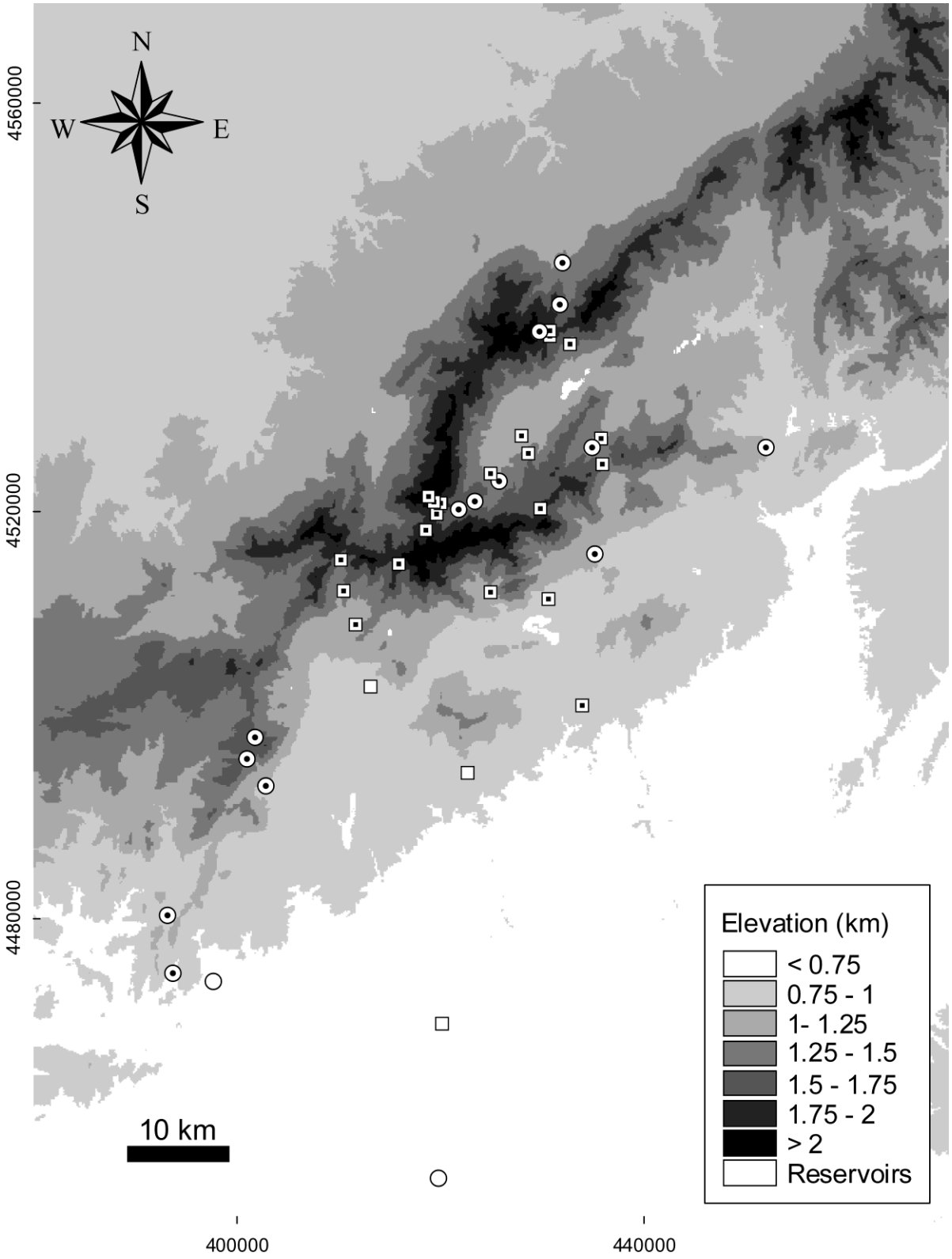

N
W
E
S
4560000
4520000
4480000
400000
440000
10 km
Elevation (km)
< 0.75
0.75 - 1
1- 1.25
1.25 - 1.5
1.5 - 1.75
1.75 - 2
> 2
Reservoirs

Figure 2

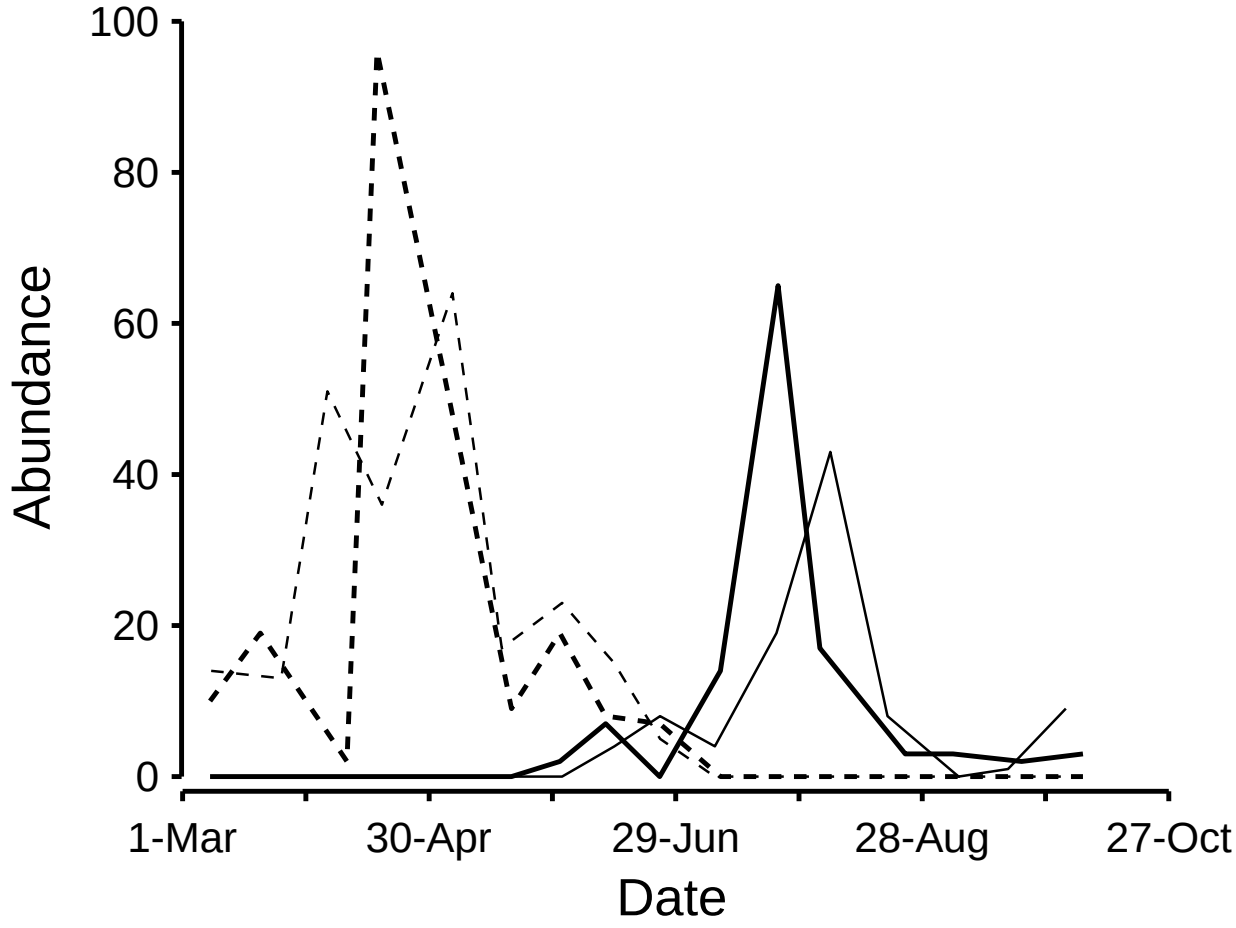


Figure 3

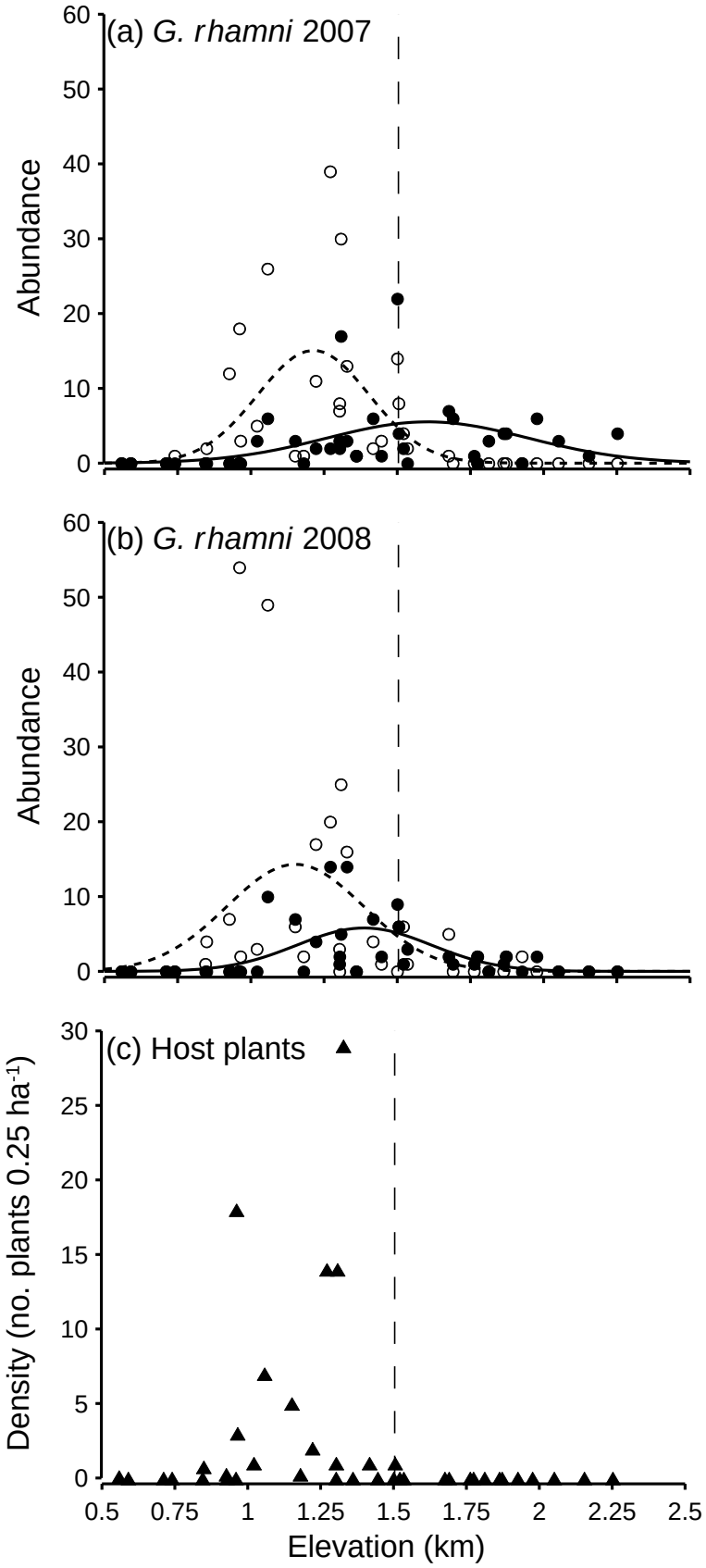
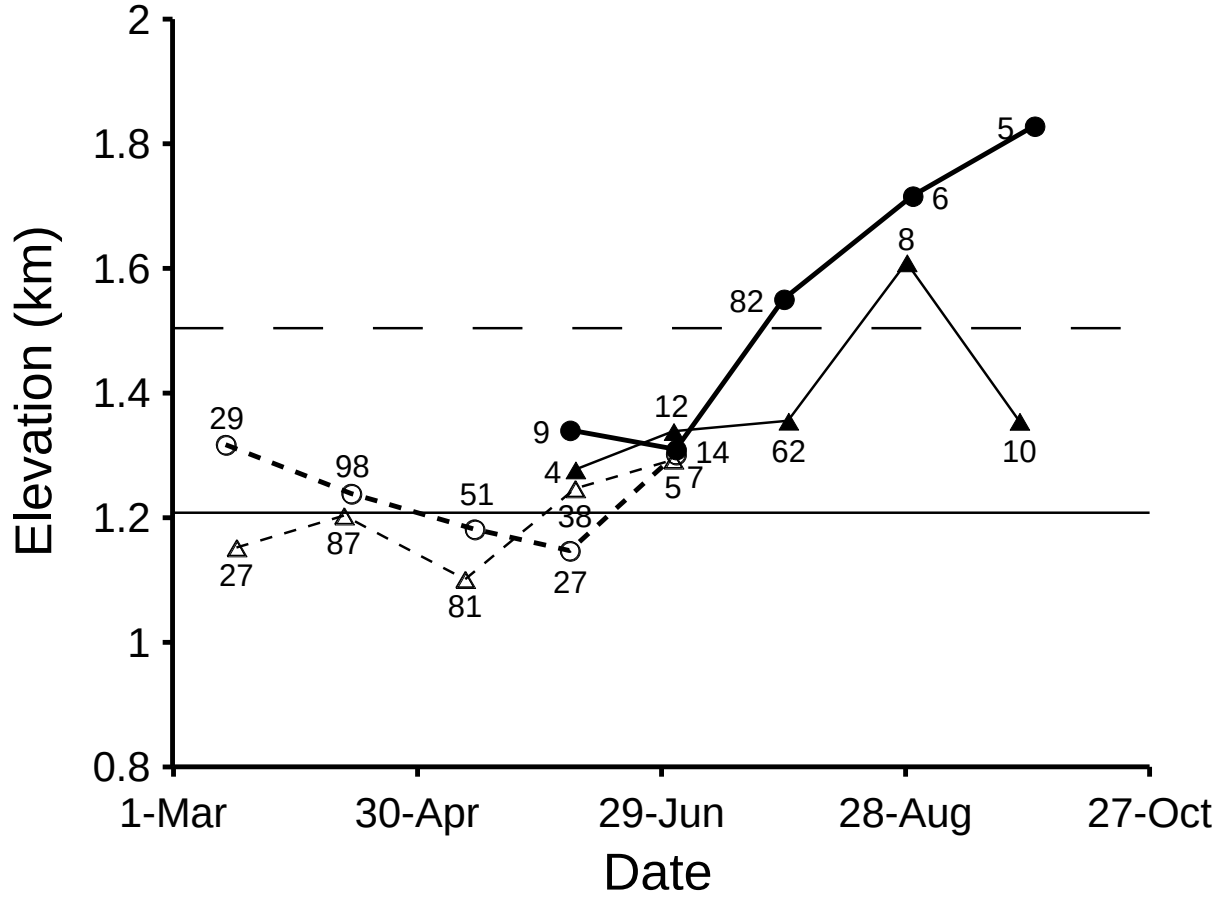

(a) G. rhamni 2007
Abundance
(b) G. rhamni 2008
Abundance
(c) Host plants
Density (no. plants 0.25 ha-1)
Elevation (km)

Figure 4


2
1.8
1.6
1.4
1.2
1
0.8
Elevation (km)
1-Mar
30-Apr
29-Jun
28-Aug
27-Oct
Date
29
98
51
27
27
87
81
9
4
12
14
82
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7
38
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62
8
6
10

Figure 5

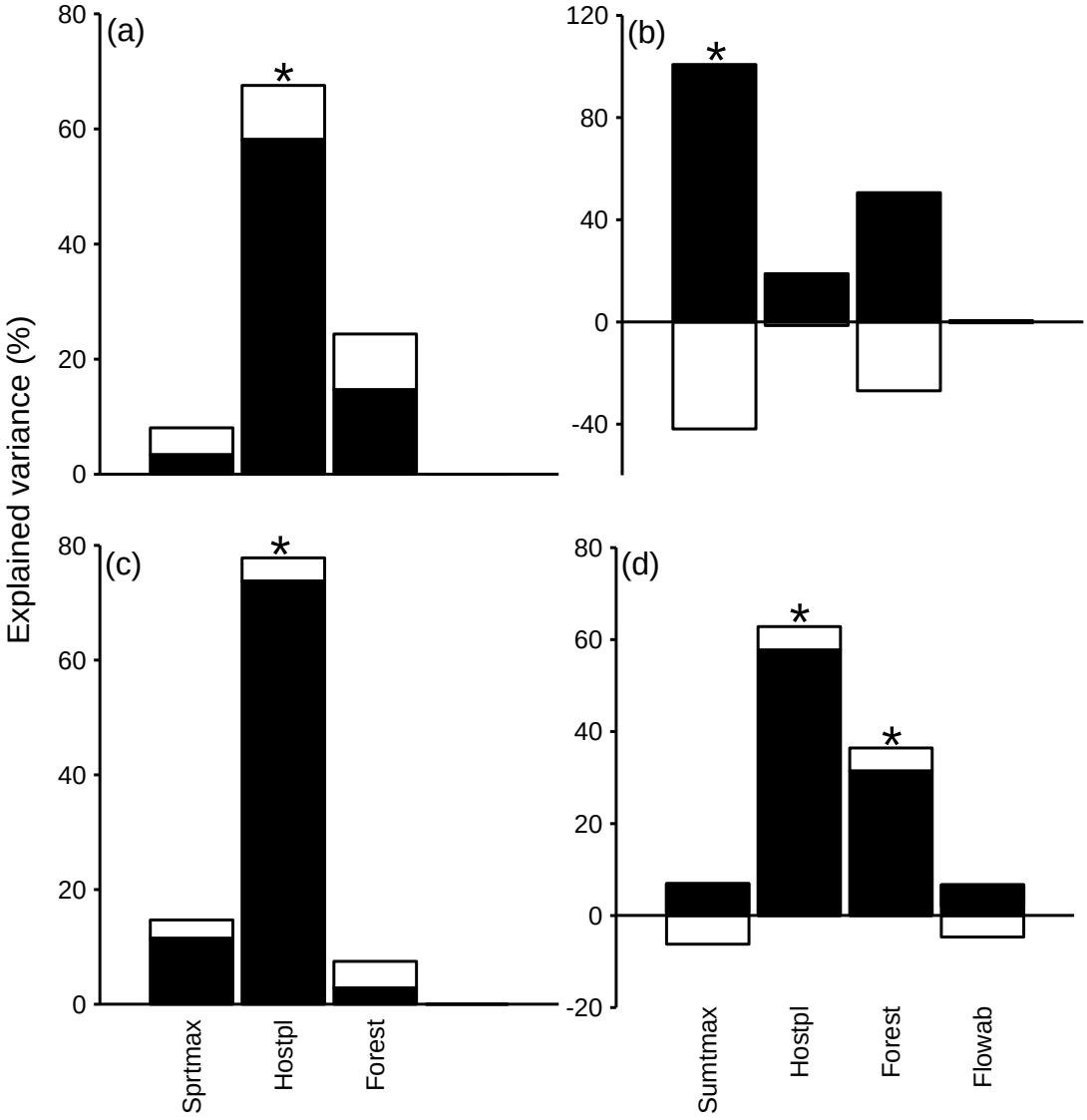
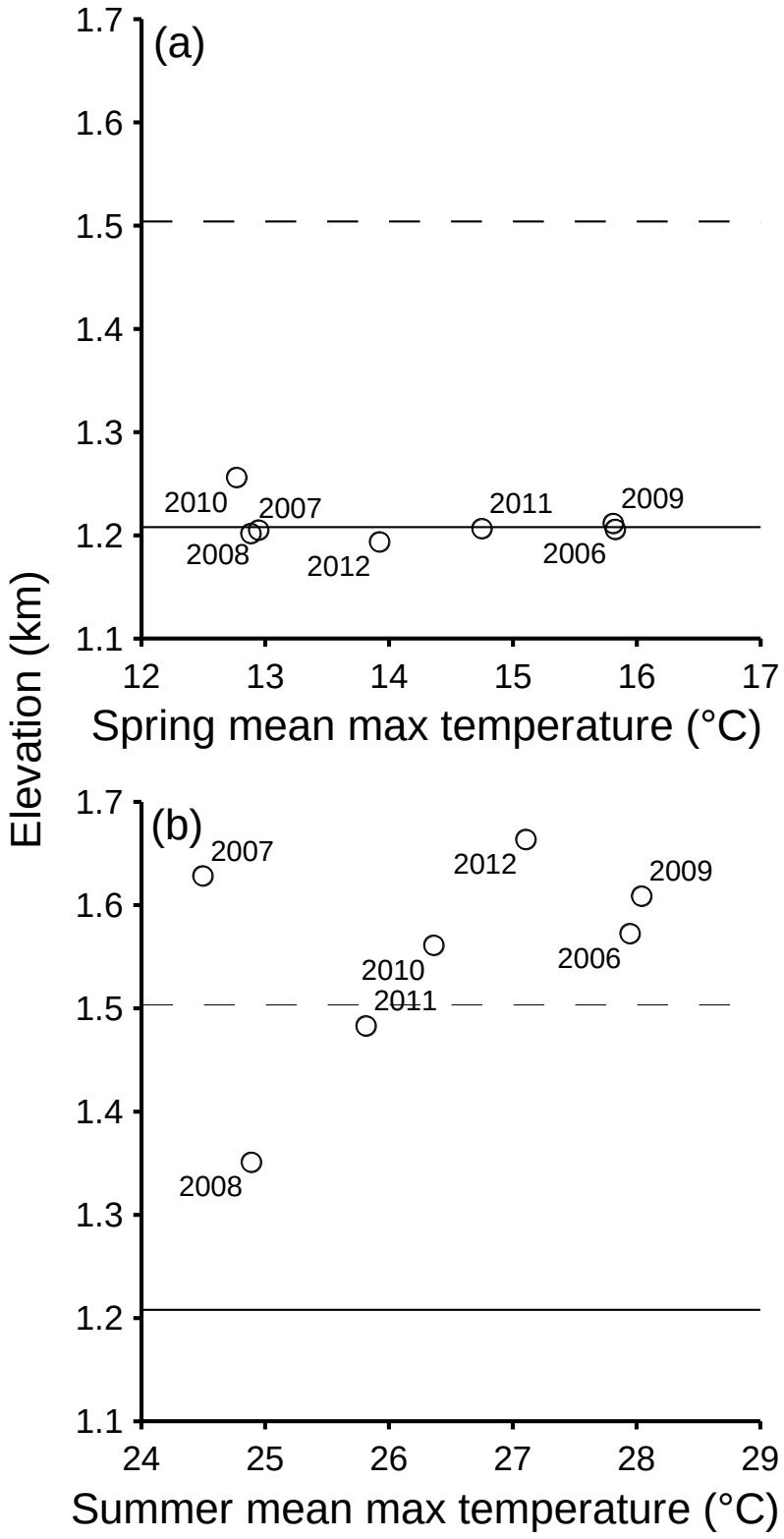

(a)
(b)
(c)
(d)
Explained variance (%)
80
60
40
20
0
120
-40
-20
*
Sprtmax
Hostpl
Forest
Sumtmax
Flowab

Figure 6


(a)
1.7
1.6
1.5
1.4
1.3
1.2
1.1
2010
2007
2008
2012
2011
2009
2006
12
13
14
15
16
17
Spring mean max temperature (°C)
Elevation (km)
(b)
2007
2012
2009
2010
2006
2011
2008
24
25
26
27
28
29
Summer mean max temperature (°C)